THE

AMERICAN NATURALIST

Vol. XLVI

December, 1912

No. 552

THE MENDELIAN INHERITANCE OF FECUND-ITY IN THE DOMESTIC FOWL¹

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The investigation here reported was concerned with the detailed analysis and interpretation of a rather extensive series of data regarding the inheritance of fecundity in the domestic fowl. The basic data are derived from trap-nest records extending over a period of years. They include records from (a) pure Barred Plymouth Rocks; (b) Cornish Indian Games; (c) the F₁ individuals obtained by reciprocally crossing these two breeds; and (d) the F₂ individuals obtained by mating the F₁'s inter se and back upon the parent forms in all possible combinations. The fully-pedigreed material made use of in the present connection includes something over a thousand adult females, each of which was trap-nested for at least one year, and many for a longer period. This material covers four generations. The birds of the fifth generation have just completed their winter records at the time of writing. Besides this fully pedigreed material, the collection and study of which has occupied

¹At the request of the editor of the AMERICAN NATURALIST the following summarized account of the principal results of an investigation carried out by the writer has been prepared. A detailed account has been published in the *Journal of Experimental Zoology*, Vol. 13, No. 2, pp. 153-268, August, 1912.

five years, there was available as a foundation, without which the results here discussed could not have been reached, nine years of continuous trap-nest records for Barred Plymouth Rocks, involving thousands of birds, which had been subjected during this long period to mass selection for increased egg production.

Altogether it may fairly be said that the material on which this work is based is (a) large in amount, (b) extensive in character, and (c) in quality as accurate as it is humanly possible to get records of the egg production of fowls.² On these accounts the facts presented seem worthy of careful consideration, and to have a permanent value quite apart from any interpretation which may be put upon them.

The essential facts brought out in this study of fecundity appear to be the following:

1. The record of fecundity of a hen, taken by and of itself alone, gives no definite, reliable indication from which the probable egg production of her daughters may be predicted. Furthermore mass selection on the basis of the fecundity records of females alone, even though long continued and stringent in character, failed completely to produce any steady change in type in the direction of selection.

2. Fecundity must, however, be inherited since (a) there are widely distinct and permanent (under ordinary breeding) differences in respect of degree of fecundity between different standard breeds of fowls commonly kept by poultrymen, and (b) a study of pedigree records of poultry at once discovers pedigree lines (in some measure inbred of course) in each of which a definite, particular degree of fecundity constantly reappears generation after generation, the "line" thus "breeding true" in this particular. With all birds (in which such a phenomenon as that noted under b occurs) kept under the same general environmental conditions such a result

² Pearl, R., "On the Accuracy of Trap-nest Records," Me. Agr. Expt. Sta. Ann. Rept. for 1911, pp. 186-193.

can only mean that the character is in some manner inherited.

The facts set forth in paragraphs 1 and 2 have been presented, and, I believe, fully substantiated by extensive evidence, in previous papers from this laboratory. It is now further shown that:

3. The basis for observed variations in fecundity is not anatomical. The number of visible occutes on the ovary bears no definite or constant relation to the actually realized egg production. This is shown by the figures presented in Table I. These give the counts of the number of oocytes on the ovary visible to the unaided eye in the case of a number of individuals. It will be understood that it is not contended that such counts give an accurate measure of the total oocyte content of the ovary. The figures, however, are so greatly in excess of what a hen actually ever lays that it may be quite safely concluded that in normal cases (where no accident or operation has induced regenerative processes in the ovary) all the eggs which will ever be laid (and usually more) are included among those visible to the eve, on an adult fowl's ovary.

From this table it is evident that when one bird has a winter record of twice what another bird has it is not because the first has twice as many oocytes in the ovary. On the contrary it appears that all birds have an anatomical endowment entirely sufficient for a very high degree of fecundity, and in point of fact quite equal to that possessed by birds which actually accomplish a high record of fecundity. Whether or not such high fecundity is actually realized evidently depends then upon the influence of additional factors beyond the anatomical basis.

4. This can only mean that observed differences (variations) in actual egg productions depend upon differences in the complex physiological mechanism concerned with the maturation of oocytes and ovulation.

TABLE 1 SHOWING THE NUMBER OF VISIBLE OGCYTES IN THE OVARY OF CERTAIN BIRDS

						D	Ovarian Count	ıt	
Bird No.	Breed	Date of Hatching	Date Killed	Winter Egg Production	Discharged Follicles	Oocytes 1 cm. or Over in Diameter	Oocytes 1 Oocytes 1 Oocytes un- cm. or Over mm.or Over der 1 mm. in Diameter in Diameter	Oocytes under 1 mm.	Total Visi- ble Oocytes
8,021	Barred Plymouth Rock	1, '10	March 28, '11	3	17	6	53	1,149	1,228
8,017	Barred Plymouth Rock	2, '10	March 30, '11	0	12	1	51	1,596	1,666
8,030	Barred Plymouth Rock	1, '10	March 10, '11	0	00	5	62	839	914
8,005	Barred Plymouth Rock	June 2, '10	March 14, '11	20	12	00	89	1,096	1,174
1,367	Barred Plymouth Rock	28, '10	April 4, '11	ಣ	49	2	29	2,121	2,306
8,018	Barred Plymouth Rock	2, '10	March 24, '11	0	23	9	42	1,123	1,194
8,009	Barred Plymouth Rock	2, '10	March 24, '11	0	17	9	49	2,029	2,101
8,010	Barred Plymouth Rock	19, '10	March 17, '11	2	24	rů	92	1,455	1,576
425	Barred Plymouth Rock	30, '08	July 7, '10	0	21	123	142	1,346	1,521
3,546	White Leghorn4	18, '09	December 26, '10		75	50	231	2,146	2,452
2,067	White Leghorn	28,	December 15, '10	32	217	-	108	3,279	3,605
3,453	White Leghorn	21,	December 13, '10		11	10	75	1,626	1,701
3,833	White Leghorn	14,	December 22, '10	0	43	10	80	2,022	2,145
52	Cornish Indian Game	21,	July 12, '10		54	9	167	1,323	1,550
7.1	F1 Cross		March 20, '11	106	50	10	20	1,875	2,000
::	Guinea hen	6.	y	:	6	63	36	717	765
	Guinea hen	٥.	January '11			cc	38	545	586

³ This includes 8 yolks in process of absorption.

* For this and the three following birds I am indebted to Professor James E. Rice, of Cornell University, who very kindly gave me these trap-nested individuals for use in the present study. The egg records in these cases are not the records for life, but the records up to November 1, 1910. The figures represent practically the total production.

Birds not in laying condition when killed.

5. A study of winter egg production (taken for practical purposes as that from the beginning of the laying year in the early fall to March 1) proves that this is the best available measure of innate capacity in respect to fecundity, primarily because it represents the laying cycle in which the widest difference exists between birds of high fecundity and those of low fecundity.

6. It is found to be the case that birds fall into three well-defined classes in respect to winter egg production. These include (a) birds with high winter records, (b) birds with low winter records, and (c) birds which do not lay at all in the winter period (as defined above). The division point between a and b for the Barred Plymouth Rock stock used in these experiments falls at a production of about 30 eggs.

7. There is a definite segregation in the Mendelian sense of the female offspring in respect to these three fecundity divisions. This is demonstrated by extensive statistics in the complete report of this work. Here a single table only may be given by way of illustration, the one chosen being taken because all three classes are represented among the progeny of the particular type of mating with which it deals.

TABLE II

Showing the Results of all Matings of Class 4 B.P.R. $\delta\delta$ × Class 1 B.P.R. QQ. Gametic Constitution: $fL_1L_2 \cdot fl_1l_2 \times fL_1L_2 \cdot Fl_1l_2$

Involved i	Individuals in Matings s Type	Win	nter Egg Pro	duction of Da	ughters	
ರ್ ರೌ	φφ	Class	Over 30	Under 30	Zero	Total Adult
4	17	Observed Expected	21 22.1	30 29.5	8 7.4	59
Mean wir	iter egg pro	oduction of all				
♀♀ in	indicated cla	ss	48.85 eggs	16.34 eggs	0 eggs	

8. High fecundity may be inherited by daughters from their sire, independent of the dam. This is proved by the numerous cases presented in the detailed evidence where the same proportion of daughters of high fecundity are produced by the same sire, whether he is mated with dams of low or of high fecundity.

9. High fecundity is not inherited by daughters from their dam. This is proved by a number of distinct and independent lines of evidence, of which the most important are: (a) continued selection of highly fecund dams does not alter in any way the mean egg production of the daughters; (b) the proportion of highly fecund daughters is the same whether the dam is of high or of low fecundity, provided both are mated to the same male; (c) the daughters of a fecund dam may show either high fecundity or low fecundity, depending upon their sire; (d) the proportion of daughters of low fecundity is the same whether the dam is of high or of low fecundity, provided both are mated to the same male.

10. A low degree of fecundity may be inherited by the daughters from either sire or dam or both.

11. The results respecting fecundity and its inheritance stated in paragraphs 3 to 10 inclusive are equally

⁶ Pearl, R., "The Relation of the Results Obtained in Breeding Poultry for Increased Egg Production to the Problem of Selection," Rpt. 30th Meeting Soc. Proc. Agr. Sci., pp. (of reprint) 1-8, 1910; "Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen,' Ann. Rpt. Amer. Breeders' Assoc., Vol. 6, pp. 317-326, 1911; "Inheritance of Fecundity in the Domestic Fowl," AMER. NAT., Vol. 45, pp. 321-345, 1911; "Breeding Poultry for Egg Production," Me. Agr. Expt. Sta. Ann. Rpt. for 1911, pp. 113-176. Pearl, R., and Surface, F. M., "Data on the Inheritance of Fecundity Obtained from the Records of Egg Production in the Daughters of '200-egg' Hens,' Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 49-84 (Bulletin 166), 1909; "Studies on the Physiology of Reproduction in the Domestic Fowl. IV. Data on Certain Factors Influencing the Fertility and Hatching of Eggs," Me. Agr. Expt. Sta. Ann. Rpt. for 1909, pp. 105-164, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production," U. S. Dept. Agr., Bur. Animal Ind. Bulletin 110, Part I, pp. 1-80, 1909; "A Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production," Ibid., Part II, pp. 81-170, 1911.

This is true, of course, only for certain gametic types of low fecundity females, as will be clear to any one who has studied the detailed evidence. This limitation, however, in nowise diminishes the force of this particular evidence in favor of the conclusion standing at the beginning of paragraph 9.

true for Barred Plymouth Rocks, Cornish Indian Games, and all cross-bred combinations of these breeds in F_1 and F_2 .

The above statements are of definite facts, supported by a mass of evidence. Their truth is objective and depends in no way upon any theory of inheritance whatsoever. With this clearly in mind we may undertake their interpretation.

It is believed that these general facts, and the detailed results on which they are based, are completely accounted for and find their correct interpretation in a simple Mendelian hypothesis respecting the inheritance of fecundity in the fowl. This hypothesis involves the following points, each of which is supported by direct and pertinent evidence derived either from physiological and statistical studies of fecundity, or from the detailed data respecting the mode of inheritance of this character.

It is assumed in this hypothesis that:

1. There are three distinct and separately inherited factors upon which fecundity in the female fowl depends.

2. The first of these factors (which may be called the anatomical) determines the presence of an ovary, the primary organ of the female sex. The letter F is used throughout to denote the presence of this factor.

3. There are two physiological factors. The first of these (denoted by L_1) is the basic physiological factor, which when present alone in a zygote with F brings about a low degree of fecundity (winter record under 30 eggs). This factor is under no limitations in gametogenesis, but may be carried in any gamete, regardless of what other factors may be also present.

4. The second physiological factor (denoted by L_2) when present in a zygote together with F and L_1 , leads to a *high* degree of fecundity (winter record over 30 eggs).

⁶ And F₃. It was thought wise to delay publication any longer in order to include the data for F₃. It may be said, however, that they are in full accord with those which have been obtained from earlier cross-bred generations and the parent forms.

When L_1 is absent, however, and L_2 is present the zygote exhibits the same general degree of fecundity (under 30) which it would if L_1 were present alone. These two independent factors L_1 and L_2 must be present together to cause high fecundity, either of them alone, whether present in one or two "doses," causing the same degree of low fecundity.

5. The second physiological factor L_2 behaves as a sex-limited (sex-correlated or sex-linked) character, in gametogenesis, according to the following rule: The factor L_2 is never borne in any gamete which also carries F. That is to say, all females which bear L_2 are heterozygous with reference to it. Any female may be either homozygous or heterozygous with respect to L_1 . Any male may be either homozygous or heterozygous with reference to either L_1 , L_2 or both.

TABLE III

CONSTITUTION OF BARRED PLYMOUTH ROCK MALES IN RESPECT TO FECUNDITY

Class	Zygote	Gametes Produced		
1	fL_1L_2 , fL_1L_2	fL_1L_2		
2	fL_1L_2 . fL_1l_2	fL_1L_2 , fL_1l_2		
3	fL_1L_2 , fl_1L_2	fL_1L_2 , fl_1L_2		
4	fL_1L_2 . fl_1l_2	fL_1L_2 , fL_1l_2 , fl_1L_2 , fl_1l_3		
5	fL_1l_2 , fL_1l_2	fL_1l_2		
6	fL_1l_2 , fl_1l_2	fL_1l_2 , fl_1l_2		
7	$f l_1L_2$. $f l_1L_2$	$f l_1 I_{c2}$		
8	$f l_1 L_2$. $f l_1 l_2$	$f l_1 L_2$, $f l_1 l_2$		
9	$f l_1 l_2$, $f l_1 l_2$	$f l_1 l_2$		

TABLE IV
CONSTITUTION OF BARRED PLYMOUTH ROCK FEMALES IN RESPECT

Class	Zygote	f-Bearing (Producing) Gametes	F-Bearing (Producing) Gametes	Probable Winter Egg Production of Q of Indicated Zygotic Constitution
1	fL_1L_2 . Fl_1l_2	fL_1L_2 , $f l_1L_2$ 9	Fl_1l_2 , FL_1l_2	Over 30 eggs
2	fL_1L_2 . FL_1l_2	fL_1L_2	FL_1l_2	Over 30 eggs
3	fL_1l_2 . Fl_1l_2	fL_1l_2 , fl_1l_2	Fl_1l_2 , FL_1l_2	Under 30 eggs
4	fL_1l_2 . FL_1l_2	fL_1l_2	FL_1l_2	Under 30 eggs
5	$f l_1 l_2$. $F l_1 l_2$	$\int l_1 l_2$	Fl_1l_2	Zero eggs
6	$f l_1 L_2$. $F l_1 l_2$	$\int l_1 L_2$	Fl_1l_2	Under 30 eggs

The reason that gametes of the type fL_1l_2 and fl_1l_2 are not formed here will be evident on consideration. Since no gametes of type FL_2 can, by

The different gametic constitutions in respect to fecundity which are to be expected in Barred Plymouth Rock males and females are shown in Tables III and IV.

Of these expected types six (1, 2, 3, 4, 7 and 8) were found and used in the experiments in the case of the males. In the case of the female class 5 birds were the only ones not actually tested out in the breeding experiments. Birds undoubtedly belonging to each of the omitted classes have been reared in the course of the experiments, but not yet submitted to continued breeding test.

The gametic constitutions of pure Cornish Indian Games in respect to fecundity are given in Tables V and VI.

 ${\bf TABLE} \ \ {\bf V}$ Constitution of Cornish Indian Game Males in Respect to Fecundity

Class	Zygote	Gametes Produced
1	fL_1l_2 . fL_1l_2	fL_1l_2
2	fL_1l_2 . fl_1l_2	fL_1l_2 , fl_1l_2
3	$f l_1 l_2$, $f l_1 l_2$	$f l_1 l_2$

TABLE VI

CONSTITUTION OF CORNISH INDIAN GAME FEMALES IN RESPECT
TO FECUNDITY

Class	Zygote	f-bearing (Froducing) Gametes	F-bearing (\$\text{Producing}\$) Gametes	Probable Winter Egg Production of Q Indicated Zygotic Constitution
1	fL_1l_2 , FL_1l_2	fL_1l_2	FL_1l_2	Under 30 eggs
2	$f l_1 l_2$. $FL_1 l_2$	$f l_1 l_2$, $f L_1 l_2$	FL_1l_2 , Fl_1l_2	Under 30 eggs
3	fL_1l_2 . Fl_1l_2	fL_1l_2 , fl_1l_2	Fl_1l_2 , FL_1l_2	Under 30 eggs
4	$f l_1 l_2$. $F l_1 l_2$	$f l_1 l_2$	Fl_1l_2	Zero eggs

It will be noted that C.I.G. Q classes 2 and 3 are gametically identical. Both are left in the table, however, since the whole table is so short that no confusion can be caused, and his example may make clear to some readers the nature of the compression (by omission of duplicate classes) which was practised in Tables III, and IV.

How well this Mendelian hypothesis agrees with the facts has been shown in detail in the complete paper. By

hypothesis, be formed this implies that an interchange of the factors L_2 and l_2 between F and f gametes can not occur. The experimental proof of the truth of this conviction has been furnished in the case of the inheritance of the barred color pattern.

way of summary the following table shows the accord between observation and expectation for all matings of each general type taken together. For reasons set forth below, the lumped figures do not give an altogether fair estimate of the matter, but some sort of a summary is necessary.

TABLE VII

Showing the Observed and Expected Distributions of Winter Egg Production for all Matings Taken Together

	Winter Production of Daughters				
Mating	Class	Over 30	Under 30	Zero	
All B.P.R. × B.P.R	Observed Expected	$365\frac{1}{2}$ 381.45	$259\frac{1}{2}$ 257.25	31 17.30	
All C.I.G. \times C.I.G	Observed Expected	2	23 25	15 15	
All $\mathbf{F_1}$	Observed Expected	36 26.5	79 86.75	8 9.75	
All F ₂ and back-crosses ¹⁰	Observed Expected	$57\frac{1}{2}$ 68.60	$98\frac{1}{2}$ 95.00	23 15.40	

Considering the nature of the material and the character dealt with it can only be concluded that the agreement between observation and hypothesis is as close as could reasonably be expected. The chief point in regard to which there is a discrepancy is in the tendency, particularly noticeable in the B. P. R. \times B. P. R. and the F_2 matings, for the observations to be in defect in the "Over 30" class and in excess in the "Zero" class. The explanation of this is undoubtedly, as has been pointed out in the detailed paper, to be found in disturbing physiological factors. The high producing hen, somewhat like the race horse, is a rather finely strung, delicate mechanism, which can be easily upset, and prevented from giving full normal expression to its inherited capacity in respect to fecundity.

The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimentally studied warrants. It must be recognized as possible, if not indeed probable, that other

 $^{^{10}\,\}mathrm{With}$ exception of one set of matings discussed in full in the complete paper.

races or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. The directions in which deviations from the plan here found to obtain may, at least a priori, most probably be expected are two. These are:
(a) differences in different breeds in respect to the absolute fecundity value of the factors which determine the expression of this character, and (b) gametic schemes which differ from those here found either in the direction of more or fewer distinct factors being concerned in the determination of fecundity, or in following a totally different type of germinal reactions.

Regarding the first point, it seems probable from the evidence in hand that the absolute fecundity value (i. e., the degree of actual fecundity determined by the presence of the gametic factor) may differ for the factor L_1 in the case of the Barred Rock as compared with the Cornish Indian Game breed. It is hoped later to take up a detailed study of this point, on the basis of the material here presented, and additional data now in process of collection. Whenever there is a difference in the absolute fecundity value of the L_1 factor, it means that the division point for the classification of winter productions should be taken at a point to correspond with the physiological Similarly, the absolute fecundity value of the excess production factor L_2 may be different in different breeds. In applying the results of this paper to the production statistics of other breeds of poultry the possibility of differences of the kind here suggested must always be kept in mind.

The second point (the possibility of gametic schemes for fecundity differing qualitatively from that found in the present study) is one on which it is idle to speculate in advance of definite investigations. I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It can not justly be urged against the conclusions of this study that the Mendelian hypothesis advanced to account for the results is so complicated, and involves the assumption of so many factors or such complex interactions and limitations of factors, as to lose all significance. As a matter of fact the whole Mendelian interpretation here set forth is an extremely simple one, involving essentially but two factors. This surely does not indicate excessive complication. To speak in mathematical terms, by way of illustration merely, it may fairly be said that the formula here used to "fit" the data has essentially the character of a true graduation formula. The number of constants (here factors) in the formula is certainly much less than the number of ordinates to be graduated.

There is no assumption made in the present Mendelian interpretation which has not been fully demonstrated by experimental work to hold in other cases. That the expression of a character may be caused by the coincident presence of two (or more) separate factors, either of which alone is unable to bring it about, has been shown for both plants¹¹ and animals by a whole series of studies in this field of biology during the last decade. To find examples one has only to turn to the standard handbooks summarizing Mendelian work, as for example those of Bateson and Baur. Again sex-linkage or correlation of characters in inheritance has been conclusively demonstrated for several characters in fowls by the careful and thorough experiments of a number of independent investigators. Finally it is to be noted that Bateson and Punnett¹² have recently shown that the inheritance of the peculiar pigmentation characteristic of the silky fowl follows a scheme which in its essentials is very similar to that here worked out for fecundity.

²¹ Particularly important here are the brilliant researches of Nilsson-Ehle on cereals, and of Baur on *Antirrhinum*.

¹³ Bateson, W., and Punnett, R. C., "The Inheritance of the Peculiar Pigmentation of the Silky Fowl," Journal of Genetics, Vol. 1, pp. 185-203.

THE SELECTION PROBLEM

The results of the present investigation have an interesting and significant bearing on the earlier selection experiments on fecundity at this station. It is now quite plain that continued selection of highly fecund females alone could not even be expected to produce a definite and steady increase in average flock production. gametic constitution of the male (in respect especially to the L_2 factor) plays so important a part in determining the fecundity of the daughters that any scheme of selection which left this out of account was really not "systematic "at all, but rather almost altogether haphazard. It is repeatedly shown in the detailed account of these experiments that the same proportion of daughters of high fecundity may be obtained from certain mothers of low fecundity as can be obtained from those of high fecundity provided that both sets of mothers are mated to males of the same gametic constitution. What gain is to be expected to accrue from selecting high laving mothers under such circumstances, at least so far as concerns the daughters?

"Selection" to the breeder means really a system of breeding. "Like produces like," and "breed the best to get the best "; these epitomize the selection doctrine of breeding. It is the simplest system conceivable. But its success as a system depends upon the existence of an equal simplicity of the phenomena of inheritance. If the mating of two animals somatically a little larger than the average always got offspring somatically a little larger than the average, breeding would certainly offer the royal road to riches. But if, as a matter of fact, as in the present case, a character is not inherited in accordance with this beautiful and childishly simple scheme, but instead is inherited in accordance with an absolutely different plan, which is of such a nature that the application of the simple selection system of breeding could not possibly have any direct effect, it would seem idle to continue to insist that the prolonged application of that system is bound to result in improvement.

It seems to me that it must be recognized frankly that whether or not continued selection of somatic variations can be expected to produce an effect on the race depends entirely on the mode of inheritance of the character selected. In other words, any systematic plan for the improvement of a race by breeding must be based and operated on a knowledge of the gametic condition and behavior of the character in which improvement is sought, rather than the somatic. Continued mass selection of somatic variations as a system of breeding, in contrast to an intelligent plan based on a knowledge of the gametic basis of a character and how it is inherited, seems to me to be very much in the same case as a man who, finding himself imprisoned in a dungeon with a securely locked and very heavy and strong door with the key on the inside, proceeded to attempt to get out by beating and kicking against the door in blind fury, rather than to take the trouble to find the location of the key and unlock the door. There is just a possibility that he could finally get out in a very few instances by the first method, but even in those cases he would be regarded by sensible men as rather a fool for his pains.

Of course what has been said is not meant to imply that selection, on the basis of somatic conditions may not have a part in a well considered system of breeding for a particular end. In many cases it certainly will have. Thus in the case of fecundity in the fowls, selection of mothers on the basis of fecundity records is essential in getting male birds homozygous with respect to L_1 and L_2 . But the point which seems particularly clear in the light of the present results is that blind mass selection, on the basis of somatic characters only, is essentially a haphazard system of breeding which may or may not be successful in changing the type in a particular case. There is nothing in the method $per\ se$ which insures such success, though that there is inherent potency in the

method per se is precisely the burden of a very great proportion of the teaching of breeding (in whatever form that teaching is done) at the present time.

It seems to me that it has never been demonstrated, up to the present time, that continued selection can do anything more than:

1. Isolate pure biotypes from a mixed population, which contains individuals of different heredity constitution in respect to the character or characters considered.

2. Bring about and perpetuate as a part of a logical system of breeding for a particular end, certain combinations of hereditary factors which would never (or very rarely) have occurred and would have been lost in the absence of such systematic selection; which combinations give rise to somatic types which may be quite different from the original types. In this way a real evolutionary change (i. e., the formation of a race of qualitatively different hereditary constitution from anything existing before) may be brought about. This can unquestionably be done for fecundity in the domestic fowl. But here "selection" is simply one part of a system of breeding, which to be successful must be based on a definite knowledge of gametic as well as somatic conditions. It is very far removed from a blind "breeding of the best to the best to get the best." The latter plan alone may, as in the case of fecundity, fail absolutely to bring about any progressive change whatever.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (i. e., its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued. To determine, by critical experiments which shall exclude beyond doubt or question such effects of selection as those noted under 1 and 2 above, whether the absolute somatic value of factors may be changed by selection, or in any other way, is one of the fundamental problems of genetics.

REFLECTIONS ON THE AUTONOMY OF BIOLOG-ICAL SCIENCE

PROFESSOR OTTO GLASER University of Michigan

Introductory

Ir the knowledge of facts and comprehension of principles by certain writers had been adequate, and others had freed their minds from the survivals of animism, the taxonomic position of biology in the scheme of knowledge would appear uncertain to no one. Prolonged and extensive inkshed however have surrounded this question with much unnecessary difficulty and confusion. Some claim that biology can not properly find a place among the sciences at all; others, that if our science is nothing more than physics and chemistry, it can have no right to independent existence; and finally, the vitalists postulate an absolute autonomy based on a specific principle.

BIOLOGICAL PREDICTION

Merz, Enriques,¹ and other present-day writers on the systematics of biology dwell at length on the fact that within the realm of the living, very strange and unexpected events take place. From the protozoans, human beings can hardly be inferred; the chromosomal complex, on account of the variations and surprising similarities of its constituent elements, fails to tell us whether we are dealing with sister species or with forms as remote as snails, frogs, ferns and mice. Because one crustacean is positively heliotropic, it does not follow that the next one, even if the species be identical, will respond in like manner, nor because one child in a family has blue eyes can we conclude that its parents or brothers and sisters have eyes of the same color. A dog or a

¹ Merz, John Theodore, "A History of European Thought in the Nineteenth Century"; Enriques, Federigo, "Probleme der Wissenschaft."

man may be friendly to-day and vicious to-morrow under similar external circumstances. Irregularities such as these, our informants tell us, should quench the ardor of the dullest, and to convince us still further of the inadequacy of our materials for science they point to rational mechanics, a domain free from ambush, and pervaded by an order in which only the foreseen and predictable find a place.

The juxtaposition of these two disciplines is not only unparliamentary, but unfortunate. Inasmuch as rational mechanics deals with abstractions and has only the slightest objective basis, it can have no materials comparable with the contents of any natural science. On the contrary, it is a method of thinking. Thinking is a phenomenon of consciousness; and consciousness, a biological event. If, therefore, the mechanic produces an orderly and coherent system in which one thing follows with certainty from another, this shows nothing else than that certain biological events, to wit, mental processes, are among the most reliable phenomena in nature.

The biologist readily concedes that he is not as weatherwise as the rational mechanic, but he does not concede that this is due either to the fundamental disorderliness of his section of nature, or because his colleague's oracular powers differ in origin from his own where he happens to possess them. As a whole man can not as vet be inferred from the protozoa, yet from the study of oxidation, secretion and digestion in unicellular organisms we could readily foresee the existence of these processes in higher forms. The conditions of the heliotropic response are such that an organism must be neither neutral nor alkaline to react positively, and one at variance with expectation can be made to do the expected by acidulation. Although half the children of brown-eyed parents may have blue eyes, this, instead of being a symptom of disorder, is in strict conformity with a law which enables us to say that two grandparents, one maternal, the other paternal, had this eye-color. The same

law makes it possible to predict the proportion and sex of color-blind persons in a family in which this defect is present. The change from friendliness to viciousness in dogs and men has been traced to definite chemical and structural changes so often that it could undoubtedly be foreseen if these were known. The embryologist foretells the hour of ovulation, the obstetrician the birth of a child, the entomologist the reappearance of a brood of locusts, the ornithologist of a flock of birds, and the ichthyologist of a school of fish, with the same reasonable certainty with which the celestial mechanic predicts the return of a comet. By the behavior of Convoluta roscoffensis, even though far from its native haunts, it is possible to tell the state of the tides. It should never be forgotten that Weismann predicted the phenomena of maturation in the germ cells.

Because the chromosomes have at present no taxonomic importance, Merz concludes that they never can have, and that biological events are therefore disorderly. It so happens that the particular facts which Merz would like to predict from these bodies are not related to what we know about them in a manner so intimate that in the present state of science prediction here would be any more reasonable than in the absence of wind to judge the weather from a bonfire. There are no reasons to doubt that if we knew accurately the chemical structure of the chromosomes, instead of merely their general composisition, number, size and shape, we could tell the species, and perhaps predict their composition in related species, much as the organic chemist predicts the make-up of one compound from another. Even now, the physiological state of the cell, and in numerous instances its kind, as well as the sex of the individual from which it was taken, can be determined from the chromosomal complex.

How the rational mechanic acquired his prophetic powers can be answered by considering the development of geometry. Are we expected to believe that from the qualities of a line, the geometrician could predict the properties of the angle between two lines, if he had vet to discover the possibility of angles? Knowing angles, he could probably tell in advance not a few of the properties of triangles, but can any one imagine, on the basis of this information alone, the relations which enable us to measure the heights of trees we have never climbed, or the distances of sun and moon? On the contrary, the history of the subject shows that the mechanist is now able to predict the motions of bodies, and the properties of configurations, not because he deals exclusively with prediction, but because he has made certain valid assumptions concerning space, and by deduction has discovered their consequences. He deals with controlled materials, but the trick of augury has no other secret than knowledge.

THE SPECIFICALLY BIOLOGICAL PROBLEM

If we reject the classification of biology necessitated by a belief in the fundamental disorderliness of its phenomena, two mutually exclusive views remain to be considered. Fortunately for the biologist the discord between them is quite unnecessary, for biology may be physics and chemistry and autonomous at the same time.

Some of the most fruitful and illuminating discussions in recent years have emanated from biological chemists and physicists, and it is hard to follow the literature on these subjects without sensing the enormous possibilities with which it is freighted. It must not be supposed, however, that proof of the purely physical-chemical nature of vital processes will show that living things are in any way different than they really are. Whether analysis can subtract qualities from things certainly seems an idle question, yet we are constantly being told that the reduction of the phenomena of life to a chemical-physical basis will demonstrate that living things are, after all, not alive!

Anatomical and histological analysis of a horse is in-

capable of showing that this animal is a cow. Even if we reduce its tissues to their constituent chemical elements, and, not content with this, continue until we have shown that a horse is entirely composed of electrons, and their activities, how could this show that a horse is not a horse? If therefore resolution can detract nothing from the things analyzed, it is clear that if these are in any way unique, they will be no less so after this process than before. The only question which can be at issue is whether living things are, or are not, unique. To this only an affirmative answer is possible.

To reason with defectives is unprofitable for they have no organ with which to perceive the qualities by which we differentiate between the organic and the inorganic. If we ask ourselves how we make this distinction we naturally think of the fact that living things are machines with the power, as Loeb puts it, of automatic self-preservation and reproduction. All the wonderful processes for which in the aggregate this simple formula stands divide animals and plants sharply from matter not alive and constitute the specific basis for the autonomy of our science. This autonomy is nothing metaphysical, or absolute, but practical, like the autonomy of physics, chemistry, astronomy and geology.

HISTORICAL BACKGROUND OF THE POSTULATED ABSOLUTE AUTONOMY

In their analyses of living things, modern biologists make use of only one practical method, but they apply it from two distinct points of view, and since the significance of phenomena in general depends on the point of view, the whole meaning of the science hangs in the balance. The validity of these theoretical standpoints, therefore, should be tested as carefully as the proposed site of an observatory.

Unfortunately the issues at stake can not be properly apprehended without some knowledge of their history. To begin with Aristotle, and the few Ionians and Eleat-

ics who preceded him, however, does not give us the needed historical background, for the impression that Aristotle was a primitive man, or that science was born in Greece, is surely wrong. Scientific knowledge began with the human race.

Although the thoughts of early men are for the most part unrecorded, study of the primitive men living to-day shows conclusively that the problem of the origin and nature of life is realized by the savage. In the lore of medicine men, magicians and seers, scientific knowledge, theories and beliefs, fuse into an alloy which, despite the varied conditions of its genesis and growth, presents remarkable homogeneity. In this cultural amalgam the attempt is made to explain the difference between a dead man and a live one, by means of "a thin unsubstantial human image, in its nature a sort of vapor, film or shadow; the cause of life and thought in the individual it animates; independently possessing the personal consciousness and volition of its corporeal owner, past or present; capable of leaving the body far behind to flash swiftly from place to place; mostly impalpable and invisible, yet also manifesting physical power, and especially appearing to men waking or asleep as a phantom separate from the body of which it bears the likeness; continuing to exist and appear to men after the death of that body; able to enter into, possess and act in the bodies of other men, of animals and even of things."2

These conclusions, drawn from the experience of dreaming, are not much more primitive than the opinions prevalent during the middle ages and surviving in the shadows of church spires to-day. Now and again, however, revolutionary teachings arose, and the most significant of these for our immediate purposes are the doctrines of René Descartes.

In his splendid history of biological theories, Rádl³ has traced with considerable detail the fortunes of the

² Tylor, Edward B., "Primitive Culture."

³ Radl, Emil, "Geschichte der Biologischen Theorien."

controversy set going in 1644 by the "Principes de la Philosophie" at a time when practically all men were vitalists. During the seventeenth and eighteenth centuries this contest engaged the ablest minds, yet mechanism achieved no decisive victory, but only an increase in the number of its followers, and the substitution of the original soul in vitalism by the life force of Müller, itself destined to elimination in the nineteenth century by supersession, largely by neglect, and by direct experiments on vital energetics.

Emil du Bois Reymond stands out as the champion of mechanism during this period, although the limitations of his materialism led him to classify the problem of life with six other insoluble riddles. Lotze overthrew the life force with arguments, substituted a purposeful preformation in the germ, and protected it from further harm by asserting that to inquire into its origin was unscientific. Fechner and Preyer attempted to clear the atmosphere by insisting that life is fundamental and the real problem the origin of the inorganic. Virchow contributed the idea of a mechanism superimposed upon that already known, and this in the hands of his successor Rindfleisch became a theory of atomic consciousness. In the seventies, however, ghostly voices fell upon deaf ears, for under the leadership of Darwin a seemingly satisfactory natural explanation of adaptation forced the mechanistic pendulum to its highest point.

While this period of scientific development proved fatal to naturalistic vitalism, metaphysical not only survived, but during the latter-day Darwinian decadence and reconstruction has again emerged, leaving behind some of the crudities of its forerunners, and apparently purged of ghosts. A change of names, however, does not constitute a change of nature. The ghosts, more rarefied than ever, are with us still, only to-day we call them Entelechies, Dominants, Psychoids and Élan Vital.

Analysis of Neo-Vitalism

Plate⁴ finds in neo-vitalism four fundamental postulates about which discussion must necessarily center. These propositions are as follows:

I. Neither now nor in the future can the organism be explained by chemistry and physics without a remainder.

II. There is an absolute distinction between dead and living matter; in the inorganic world the law of causation holds, but in the organic causation holds together with a unique law.

III. The uniqueness expresses itself in this, that every organic process is final (teleological), that is, governed by immanent purposefulness.

IV. The cause of this finality, in so far as the vitalists are not agnostic, is (a) a psychical factor; (b) a metaphysical factor.

POSTULATE I

Neither now nor in the future can the organism be explained by chemistry and physics without a remainder.

Nothing could be more physical and chemical than the analysis of the whole universe into a system of electrons. When such resolution has been accomplished and every known chemical element has been shown to be a special case of corpuscular movement, the organic world and all that characterizes it will be expressible in terms of electrons if this mode of expression should appear serviceable. Would it not remain true, however, that hydrogen is hydrogen, and oxygen, oxygen? Even if these gases were proved to be configurations of essentially similar corpuscles, they would nevertheless continue to be individually different, and those so inclined would find it possible to found separate sciences of hydrogenology and of oxygenology, and these subjects would be autonomous. Does any one conclude from this that the mechanist is not fit to deal with these matters? Or that his methods are fundamentally inadequate? Yet the argu-

⁴ Plate, Ludwig, "Darwinsches Selektionsprincip," 3d ed.

ment of those who would cast mechanism out of biology is identical. Resolution leaves intact uniqueness wherever found, and the declaration that this is true of the organism is a platitude.

POSTULATE II

There is an absolute distinction between dead and living matter; in the inorganic world, the law of causation holds, but in the organic, causation holds together with a unique law.

The second part of this proposition will be considered in connection with postulate III. To the first part the mechanist subscribes heartily, but adds that in his experience the distinction between hydrogen and oxygen is equally absolute.

POSTULATE III

The uniqueness expresses itself in this, that every organic process is final (teleological); that is, governed by immanent purposefulness.

In discussing postulate III, all that is needed is (a) to sound its logical consequences; (b) to inquire how it agrees with observations on individual and racial finality; and lastly, (c) to expose the psychology of the teleological idea itself.

(a) From the harmony between the organic and the inorganic, Driesch concludes that "nature is nature for a purpose." If the whole universe, however, is governed by immanent purposefulness what becomes of the distinction between the organic and the inorganic? In a purposive system the teleological nature of any particular event or group of events can not be inferred, for purposefulness can only be recognized by comparison with purposelessness. Thus general teleology denies the existence of half the materials for the inference of the very thing on which it bases itself, and with the best intentions in the world, and without in any way seeming to sense it, vitalists themselves have not only disarmed

teleology in the realm of the living, but have made the principle scientifically impossible.

(b) Were every organic event final or purposeful, functional adjustment, training and education would be unnecessary and impossible. Jennings⁵ tells us:

How the relations that impress us as teleological were brought about, constitutes undoubtedly a set of most difficult problems. But to keep us from despairing, we find this process taking place in the lives of individuals in a manner that can readily be studied. This is in the formation of habits. In the formation of habits, we see that the organism at first does not react in a way that impresses us as teleological, while later it does, and we can watch the process change from one condition to the other, and discover how it is causally determined. Since then a method of action that appears to us teleological is produced in an intelligible way under our very eyes, in the lifetime of the individual, there is no reason why we may not expect to find out how teleological relations have been brought about in the life of the race when we have actually made a start in the study of the physiology of racial processes. It seems clear that the apparent relation of a present process or structure to something that comes later in time is always due to the fact that this future something has in fact acted upon the organism in the past. The present condition fits the future condition only because of a certain constancy in the universe, through which the "something past" reappears again in the future.

The ability to make functional adjustments of this character is only a special case of automatic self-preservation, and is found in all organisms because those devoid of it are for this very reason eliminated and consequently remain largely unknown. Paleontology is the science that deals chiefly with these failures. How many organisms have been unable to make the necessary adjustments is attested by the great number of extinct animals and plants; how many are failing to-day is shown by every rapidly vanishing species, as well as by many experiments and special observations. Several of the mutants of de Vries have for one reason or another

⁵ Jennings, Herbert S., "Diverse Ideals and Divergent Conclusions in the Study of Behavior in Lower Organisms," American Journal Psychology, Vol. XXI.

⁶ Loeb, Jacques, "The Mechanistic Conception of Life," Pop. Sci. Mo., Vol. LXXX.

proved indurable, whereas Loeb⁶ has pointed out that faulty organisms must frequently arise, although we only become aware of them under exceptional conditions.

Moenkhaus found ten years ago that it is possible to fertilize the egg of each marine bony fish with sperm of practically any other marine bony fish. His embryos apparently lived only a very short time. This year I succeeded in keeping such hybrid embryos between distantly related bony fish alive for over a month. It is therefore clear that it is possible to cross practically any marine teleost with any other.

The number of teleosts at present in existence is about 10,000. If we accomplish all possible hybridization 100,000,000 different crosses will result. Of these teleosts only a very small proportion, namely, about one one-hundredth of one per cent., can live. It turned out in my experiments that the heterogeneous hybrids between bony fishes formed eyes, brains, ears, fins and pulsating hearts, blood and blood vessels, but could live only a limited time because no blood circulation was established at all—in spite of the fact that the heart beat for weeks—or that the circulation, if it was established at all, did not last long.

The possibility of hybridization goes much further than we have thus far assumed. We can cause the eggs of echinoderms to develop with the sperm of very distant forms, even mollusks and worms (Kupelwieser): but such hybridizations never lead to the formation of durable organisms.

It is therefore no exaggeration to state that the number of species existing to-day is only an infinitely small fraction of those which can and possibly occasionally do originate, but which escape our notice because they can not live and reproduce. Only that limited fraction of species can exist which possesses no coarse disharmonies in its automatic mechanism of preservation and reproduction. Disharmonies and faulty attempts in nature are the rule, the harmonically developed systems the rare exception. But since we only perceive the latter we gain the erroneous impression that the "adaptation of the parts to the plan of the whole" is a general and specific characteristic of animate nature, whereby the latter differs from inanimate nature.

If the structure and the mechanism of the atoms were known to us we should probably also get an insight into a world of wonderful harmonies and apparent adaptations of the parts to the whole. But in this case we should quickly understand that the chemical elements are only the few durable systems among a large number of possible but not durable combinations.

(c) Overlooking for the moment the obvious difficulties of the assumption, we can be certain that the idea of teleology would never have entered the biologist's head were he not himself a living thing. Since this is the case, however, his interest in life exceeds all others, and he attends to the processes that make life possible only because of their resultant. Inasmuch as the latter occupies the focus of his mind, he wrongfully reasons backward from results to processes, and finding in these none that might have rendered the cherished product impossible, concludes that the processes were all along aiming at what, from his standpoint, is the end. Clearly the conclusion has only an anthropocentric basis.

POSTULATE IV

The cause of this finality, in so far as the vitalists are not agnostic, is (a) a psychical factor; (b) a metaphysical factor.

Since biological finality is an anthropomorphism, a discussion of the supposed teleological factors is futile. Inasmuch, however, as psycho-vitalism has its counterpart in psycho-mechanism, the fallacy common to both

may be pointed out.

- (a) To reflect mind into the cell, and so reflected to use it as an explanation of what the cell does, is the method of primitive animism. Quite apart from the fact that the existence of mind, so far, at least, has been demonstrated only in the case of certain higher animals, but not at all for the lower, or the developmental stages of the higher, as an explanation it can have no title to serious consideration since it is itself one of the elements of the automatic self-preservation which it is the aim of biology to analyze. To interpret something we do not understand in terms of something else which at present we understand even less, may give temporary comfort to some minds, but the ideals of scientific explanation call for the reverse process.
- (b) The difficulties of Driesch's style are such that many biologists refuse to read his books. For this rea-

son I have made from one of them⁷ a series of extracts to serve as illustrative material. The italics are not mine.

Driesch's Entelechy

Entelechy or the psychoid has nothing of a "psychical" nature. (P. 138.)

We indeed are in a rather desperate condition with regard to the real analysis of the fundamental properties of morphogenetic, adaptive, and instinctive entelechies: for there must be a something in them that has an analogy, not to knowing and willing in general, as it may be supposed to exist in the primary faculties of psychoids, but to the willing of specific unexperienced realities, and to knowing the specific means of attaining them. (P. 142.)

To build up the organism as a combined body of a typical style is the task of entelechy; entelechy means the faculty of achieving a "forma essentialis"; being and becoming are here united in a most remarkable manner; time enters into the Timeless, i. e., into the "idea" in the sense of Plato. (P. 149.)

There is first the entelechia morphogenetica, and after that the entelechia psychoidea and the latter may be discriminated as governing instincts and actions separately. Furthermore the different parts of the brain, such as the hemispheres and the cerebellum in vertebrates, may be said to possess their different kinds of entelechy.

In fact we may speak of an order concerning the rank or dignity of entelechies, comparable with the order of ranks or dignities in an army or administration. But all entelechies have originated from the primordial one and in *this* respect may be said to be one altogether.

Now the primordial entelechy of the egg not only creates derived entelechies, but also builds up all sorts of arrangements of a truly mechanical character; the eye, in a great part of its functioning is nothing but a camera obscura, and the skeleton obeys the laws of inorganic statics. Every part of these organic systems has been placed by entelechy where it must be placed to act well in the service of the whole, but the part itself acts like a part of a machine.

So we see finally that the different forms of harmony in the origin and function of parts that are not immediately dependent on one another, are in the last resort the consequence of entelechian acts. The entelechy that created them all was harmonious in its intensive manifoldness; the extensive structures which are produced by it are therefore harmonious too. In other words there are many processes in the organism which are of the statical-teleological type, which go on teleologically or purposefully on a fixed machine-like basis, but entelechy

[†]Driesch, Hans, "The Science and Philosophy of the Organism," Gifford Lectures, 1908.

has created this basis, and so statical teleology has its source in dynamical teleology.

We now see the full meaning of the statement that entelechy is an "intensive manifoldness" realizing itself extensively; in other words, we know what it means to say that a body in nature is a living organism; we have given a full descriptive definition of this concept. (Pp. 150-151.)

Any *single* spatial occurrence induced or modified by entelechy has its previous *single* correlate in a certain *single* feature of entelechy as far as it is an intensive manifoldness. (P. 154.)

Entelechy may be aroused to manifestation by a change in bodily nature, such as is effected by fertilization, or by some operation, or by some motor stimulus; on the other hand, entelechy may on its own part lead to changes in bodily nature. (P. 156.)

It is the essence of an entelechy to manifest itself in an extensive manifoldness: all the details of this extensive manifoldness depend upon the intensive manifoldness of the entelechy, but not upon different spatial "causes." (P. 157.)

Entelechy lacks all the characteristics of quantity; entelechy is order of relation and absolutely nothing else; all the quantities concerned in its manifestations in every case being due to means which are used by entelechy, or to conditions which can not be avoided. (P. 169.)

Entelechy, as far as we know, at least, is limited in its acting by many specificities of inorganic nature, among which are the specificities included under the phrase "chemical element." (P. 179.)

Enteleehy is also unable to cause reactions between chemical compounds which never are known to react in the inorganic world. In short entelechy is altogether unable to create differences of intensity of any kind.

But enteleehy is able, so far as we know from the facts concerned in restitution and adaptation, to suspend for as long a period as it wants any one of all the reactions which are possible with such compounds as are present, and which would happen without entelechy. (P. 180.)

Entelectly though not capable of enlarging the amount of diversity of composition of a given system, is capable of augmenting its diversity of distribution in a regulatory manner, and it does so by transforming a system of equally distributed potentialities into a system of actualities which are unequally distributed. (P. 192.)

Entelechy . . . is a factor in nature which acts teleologically. It is an intensive manifoldness and on account of its inherent diversities it is able to augment the amount of diversity in the inorganic world as far as distribution is concerned. It acts by suspending and setting free reactions based upon potential differences regulatively. There is nothing like it in inorganic nature. (P. 205.)

Entelechy is an elemental factor of *nature* conceived to explain a certain class of natural phenomena. (P. 206.)

You may say if you like that entelectly, when turning a mass particle, acts upon it at right angles to its path—this kind of action requiring no energy, but even thus there would be only a pseudo-obedience to the laws of real mechanics, since entelectly must be regarded here as non-energetical and as interfering with inertia at the same time. (P. 223.) Entelectly is affected by the accomplishment of its own performance, in acting as well as in morphogenesis. (P. 228.)

In order that adaptation may happen, the fundamental state of the organism must be disturbed in its normality; this fact affects or calls forth entelechy. (P. 229.)

Entelechy is affected and thus called into activity by changes of any normality governed by it which are due to external causes and these changes do not affect entelechy as a mere sum of changed singularities, but as changes of normality as a whole. (P. 232.)

Entelechy is affected by and acts upon spatial causality as if it came out of an ultra-spatial dimension; it does not act in space, but it acts into space. (P. 235.)

Entelechy is an agent acting manifoldly without being itself manifold in space or extensity. Entelechy then is only an agent that arranges, but not an agent that possesses quantity. (P. 250.)

Entelechy is something different from matter and altogether opposed to the causality of matter. (P. 255.)

May not entelectly be called a "substance" in the most general philosophical sense of the word, that is, in the sense of a something irreducible, which remains the always unchangeable bearer of its changeable qualities. (P. 256.)

Entelectly has the power of preserving its specific intensive manifoldness in spite of being divided into two or more parts. (P. 257.)

Entelechy therefore can not possess a "seat." (P. 258.)

At present the question whether entelechy is a "substance" must remain as open as the previous question about the relation of entelechy to causality. . . . Entelechy was a kind of "quasi" causality, and now may be said to be an enduring "quasi-substance." (P. 260.)

Entelechies, though transcending the realm of the Imaginable, do not by reason of their logical character as such form constituents of metaphysics in the sense of something absolute and independent of a subject. (P. 320.)

Entelechy is alien not only to matter but also to its own material purposes. (P. 336.)

Mir wird vor alle Dem so dumm Als ging mir ein Mühlrad im Kopf herum!

CONCLUSION

I have tried to show that biological events are orderly; that a distinct problem guarantees the autonomy of the science: that the application of physical and chemical methods has no shortcomings specifically different from those met with when applied to the inorganic, and finally that vitalism in addition to being unnecessary is absurd. The question whether the modern outburst of metaphysical biology, a movement which finds favor among philosophers and psychologists, and has no small following among zoologists and botanists, is not, despite its obvious faults, sound in motive, remains to be answered. Mechanical methods, even if applicable to vital events no less than to any others, might nevertheless possess an inherent weakness discoverable only when enlisted in biological service. The only reply possible to this question is that they are the best methods which human beings can devise, for their excellencies are grounded in our structure, their deficiencies in that of the world outside.

It has been pointed out over and over again that the explanations of science never amount to more than the enumeration of the conditions under which the events in nature take place. With ultimate explanation science does not deal, not because men of science do not want to, but because in their experience nature contains nothing ultimate. The failure, therefore, of science to give us more than it does can be held up as a fault only by those who are dissatisfied with the structure of the universe. For this feeling intellectual hygiene is the only cure.

If the limitations of scientific methods are to be found in the limitations of a limitless universe, their excellencies, as instruments for the automatic preservation of life, are to be found in ourselves, for the mechanical symbols by the aid of which natural phenomena are interpreted are the easiest for us to use. The value of these symbols depends on our power to visualize, and visualization depends on sight. Is it without significance in this connection that the eye begins in the embryo earlier than any other receptor of special sense, or that sight, except perhaps by a few poets and musicians, is acclaimed the most priceless of all our senses?

If we lived in a world of phantasms, the value of sight would largely disappear, for, as Berkeleys has pointed out, it is an organ of anticipatory touch upon which depends our ability to avoid harmful collisions, and to bring about desirable ones. From the very beginning of our lives we see and deal with visible objects. Is it strange then that we should attempt to express all our experience in terms of the language which by our very structure and history is the most used and hence the most efficient medium of interpretation we possess?

Modern energetics has indeed discarded solid molecules and atoms, and has replaced these by constellations of electrons, yet even if the electrons are nothing more than electrical charges, they are believed to possess mass, and to have certain properties in common with visible things. Does not the physicist still draw pictures on the wall to make clear what he means? Is not a picture a visual symbol by the aid of which we understand a less familiar one? Escape is impossible, for mechanistic symbolism is grounded in our very nature, and for this reason its employment rises to the dignity of a moral act, for it involves neither more nor less than the application of our best capabilities to the best of all purposes—the interpretation of nature.

Berkeley, George, "An Essay Towards a New Theory of Vision,"

THE SPAWNING HABITS OF THE SEA LAMPREY, PETROMYZON MARINUS¹

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The spawning habits of several species of lamprev are known from observations which have been made in both Europe and America.² Those of the sea lamprey, Petro. myzon marinus, however, have not been studied, notwithstanding that this is the largest of the lampreys and is common to both sides of the Atlantic. It is merely known that this species ascends rivers for the purpose of spawning; and that the "fish" transport stones in building their nest much like other lamprevs (Burroughs, '83; Holder, '85). In 1883 a French observer, L. Ferry ('83), noted the development of sea lamprey eggs taken directly from a female specimen. He concluded that the eggs must already have been fertilized, and hence that fertilization in the lamprevs is internal. This conclusion. in the light of the careful observations on the spawning of various lampreys, especially Petromyzon planeri and Lampetra wilderi, is undoubtedly erroneous. Moreover, the discovery that lamprey eggs can develop parthenogenetically (Bataillon, '03), affords a simple explanation of the facts recorded by Ferry. None the less the observation of the breeding habits of the sea lamprey was very desirable.

The observations recorded in this paper were made by the writer on Long Island, June 1 and 2, 1911, while collecting material for a group to represent the nesting habits of the sea lamprey in the American Museum of Natural History. The locality, Smithtown, on the Nissequegue River, Long Island, was suggested to me by

¹Read before the American Society of Zoologists, at Princeton, N. J., Dec. 27, 1911.

² See annotated bibliography at end of paper.

Professor Bashford Dean, who had learnt of it through Dr. Tarleton H. Bean.

Locality and Date of Observation.—At the date of these observations, June 1 and 2, 1911, lampreys had been seen in the Nissequogue River for several days. A number of abandoned, partly scattered nests were also to be found; hence June 1, appears to be toward the end of the spawning season, which for Long Island must be put down as the latter half of May.



Fig. 1. Sea Lampreys, *Petromyzon marinus*, on a Nest. An exhibition group, 4 by 5 feet, in the American Museum of Natural History; prepared under the supervision of the writer.

The Nissequogue is a small stream which empties into Long Island Sound. At the village of Smithtown, three and a half miles from its mouth, it is shallow (a foot or two deep), perfectly clear, and flows over a bed of large, water-stained pebbles. Here and there are patches of "river grass." The water is perfectly fresh here, although still affected by the tide. A quarter of a mile above and below the village bridge, the river grows

deeper and muddier; my observations were therefore confined to the pebbly portion, a stretch of about half a mile. Here a dozen nests were found, four with lampreys on them, the others deserted and partly scattered by the tide.

Nests.—The nest of the sea lamprey is similar to that of other species, but much larger. It is a circular depression in the river bed, two to three feet in diameter. One that was measured was two feet three inches across, and six inches deep in the center. The



FIG. 2. THREE SPECIMENS OF *Petromyzon marinus* on a Nest. Instantaneous photograph taken without special apparatus in bright sunlight, at low tide, with only three or four inches of water above the "fish." One male and two females. (Not retouched.)

nests are easily recognized, even at a distance of several feet, by the large number of whitish quartz pebbles which have been uprooted and turned with their clean faces up. They are built at random anywhere in the river: near the bank, in the shade of overhanging trees; in the middle of the stream, exposed to the glare of the sun; or even, as with the nest shown in the figures

(Figs. 1 and 4), partly under a log. Occasionally two nests adjoin so that their peripheries overlap.

Standing in the water close to a nest, one may observe minutely every movement the lampreys make. One may even stroke them or lift them by the tail without disturbing them. A "fish" must be raised to a considerable angle before it will loosen its hold on the stone to which it clings, and dart away; and then it will go only a short distance, fifty or a hundred feet, and seek refuge under the "river grass."

The manner of building the nest is quite like that of the



FIG. 3. Freshly dead lamprey clinging to a stone by the vacuum produced in the buccal funnel when the mouth is pressed against it.

brook lamprev (Lampetra wilderi), as described by Gage ('93), and by Dean and Sumner ('97). But owing to the large size of the species all the processes are writ large, as it were, so that one can see the purpose of every movement. Building the nest consists in carrying the pebbles and stones out of a circular area until a basin-like depression is formed. As the work proceeds the finer material in the interstices between the pebbles gradually accumulates, so that the bottom of the nest becomes covered with sand and fine gravel. The stones are seized with the circular mouth to which they cling entirely by suction. The "teeth" play no part in this work, as may be proved by experimenting with the freshly dead "fish." By pressing the mouth of such a "fish" against a stone, it may be made to hold on so tenaciously, that by lifting the stone one lifts the fish (Fig. 3). A vacuum is

produced inside the buccal funnel, and this is the immediate cause of the hold. In carrying stones out of the nest, the procedure varies with the size of the stone. Small stones, an inch or two across, are picked up in the

mouth and carried out. Larger stones, firmly rooted in the bottom, require considerable effort to be dislodged; the stone is tugged upward, the lamprey receding backward in a straight line. Sometimes instead of pulling backward, the lamprey charges head-on and pushes the stone in front of it up the incline, the body remaining rigid and acting as a lever, while the tail is lashed vio-

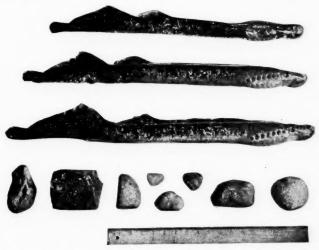


Fig. 4. Same Three Specimens as Shown in Fig. 2, Photographed shortly after they were taken from the Nest. Upper two, females; lowest one, a male. The stones in lower half of photograph were picked up just as they were carried by the lampreys out of the nest. The half brick shown in the picture weighs 840 grams.

lently to gain a firmer support. Some of the larger stones carried by the lampreys out of the nest (Fig. 4), were picked up just as they were released from the mouth; they were found to weigh (in air) from 145 to 840 grams.

The building and improving of the nest go on continuously between intervals of mating. Both the male and the female take part in this work. On one nest there were observed a male and a female; they were joined now and then, for some minutes, by a second female which

had been for some time by herself on an adjoining nest. During the time the three "fish" were on the one nest (Figs. 2 and 5) they all took part in repairing it, in the intervals between mating—the male apparently not distinguishing between the female of his own nest and the intruder. In two other cases there was one individual to a nest. After carrying a stone out the lamprey immediately returns for another. This is repeated a number of times and then the lamprey clings to a stone apparently exhausted (Fig. 4). Now and then the tail is lashed against the sides of the nest to pad it down. When on a nest by itself, a lamprey occasionally wanders a distance of some feet-even several hundred feet-but invariably returns to continue its nest-building. These wanderings are perhaps for the purpose of finding a mate.

Mating.—The method of copulation is similar to that of the brook lamprey, Lampetra wilderi, as described by Dean and Summer ('97); and it is unnecessary to redescribe it here. I will merely comment on a few de-The female must cling to a large stone in the nest in order that copulation take place. seizes her by the top of the head. In copulo, the two are arranged so as to form an ellipse. The caudal portion of the male is applied immediately back of the first dorsal of the female, and curved in a loop around her body. Several authors have referred, in the case of both American and European lampreys, to the vibration of the posterior portions of the "fish," in copulo. In the sea lamprev this vibration may be observed very closely. It lasts two or three seconds. It begins slowly, gradually increases in frequency until it reaches an exceeding rapidity of vibration, then subsides by a few slow beats. The motion strongly suggests the vibration of a rattlesnake's tail in the warning pose. Indeed while watching the lampreys one can hardly keep from imagining the sound which ought to accompany the lamprevs' vibrations, so similar is the movement to that of the rattle-snake's tail.

As to the length of time "fish" on a nest continue to spawn, I was able to make some observations. The nest shown in Figs. 1 and 4 was observed continuously for over four hours, from 10 a.m. until after 2 p.m.; and during that time copulation took place at intervals of from a few to ten minutes; and in all probability would have continued several hours longer had the



FIG. 5. THE SAME NEST AS IN FIG. 2, SHOWING TWO OF THE SPECIMENS in copulo. The head of the male is seen protruding from under the log directly under the arrow; his body is hidden by the log and his tail is looped around the female. The second female is seen clinging to a stone. (Not retouched.)

"fish" been left on the nest. Both became gradually more and more scarred from seizing each other with their mouths: round pale wounds stood out clearly against the blue-black of the head of the female where the male had repeatedly seized her; and large whitish wounds could be seen on her back, especially posterior to the first dorsal fin. The male likewise was scarred in several places on the head and back. These scars are

greatly augmented through continual rubbing against stones, padding down the nest, etc.

Fate of Sea Lampreys After Spawning.—From the facts at hand, it appears that lampreys that go up the river to spawn do not again return to the sea, but die shortly after spawning. I found two dead, badly scarred, spent lampreys in the river not far from deserted nests. One was in the shade of tall grass near the bank, the other tangled in weeds and twigs in the middle of the river. Both had been rasped, apparently for food, by other lampreys. Burroughs ('83), also records that it is not unusual to find dead lampreys in June.

The causes of the death of these lampreys—and indeed of all anadromous fishes—are still rather obscure. Death is probably chiefly due to the cycle of katabolic processes initiated on the maturing of the gonadial products. Besides this at least two other causes must be regarded as contributary: first the greatly lessened vitality due to the constant exertion in uprooting and transporting stones. Lampreys thus weakened become the prey of other lampreys. Secondly, the numerous scars or wounds which they inflict on one another in mating allow "fungus" to invade, and ultimately to destroy, their tissues. All three of these causes, probably, play a part in causing the death of the sea lampreys after spawning.

Remarks on the Senses and Mentality of the Sea Lamprey.—The behavior of the lampreys was carefully noted to see in how far their senses come into play in building the nest and in other activities. The general impression was that the sea lamprey is guided by touch more than by any other sense. Sound does not disturb them while on the nest: one may carry on a conversation right over a nest without in the least affecting them. Indeed one lamprey that was building a nest under a wooden bridge was not disturbed by the clattering of automobiles over it. This insensitiveness to sound may mean,

however, merely absorption in the work of nest-building, and not that the lampreys are insensible to this stimulus.

The eyes of lampreys in the water shine like black beads; but they are not very sensitive. If one meets a lamprey swimming toward him in the river, it will come almost right up before it will discover the person and turn aside.

Many of the movements of the sea lamprey on the nest are purposeless—as was noted also for the brook lamprey by Dean and Summer ('97). Thus a lamprey will sometimes pick up a stone outside the nest, carry and drop it into the nest; or while carrying out a stone, will drop it half way up the side of the nest. It will tug at a large stone which it cannot possibly dislodge, or at a log, in an effort to drag it out of the nest, and will repeat this again and again, without profiting in the least by previous failures. On the whole one has a feeling that the lamprey possesses a very low mentality even as compared with fishes.

ANNOTATED BIBLIOGRAPHY

The following list includes all the papers I have been able to find that deal with the spawning habits of lampreys. Those having to do with the cytology of fertilization are listed in Ziegler's text-book referred to below.

Bataillon, E.

- 1903. La segmentation parthénogénétique expérimentale chez les œufs de Petromyzon planeri. Comp. Rend. Acad. Sci., Vol. 137, pp. 79-80.
 - Carried embryos as far as the blastula stage—"en plongeant et maintenant les œufs dans des solutions de saccharose à 5 ou 6 pour 100 ou dans des solutions isotoniques de NaCl."

Burroughs, John. 1883. A lamprey's nest. The Century Magazine, XXV, p. 457.

Observed Petromyzon marinus spawning in a creek. Describes their mode of transporting stones; their indifference to an observer at close range; but does not describe the nest, nor apparently recognizes the purpose for which the stones are transported. The female is the larger of the two. "In June it is not unusual to find their dead bodies in the streams they inhabit."

Dean, Bashford, and Sumner, Francis B.

1897. Notes on the spawning habits of the brook lamprey (Petromyzon wilderi). Trans. N. Y. Acad. Sci., XVI, pp. 321-324, Pl. XXVII.

Detailed observations on manner of building nest, on copulation, and general behavior. Contains the best figure extant of lamprevs on nest.

Ferry, L.

1883. Sur la lamproie marine. Compt. Rend. Acad. Sci., pp. 721-723. Translated, in part, in Ann. Mag. Nat. Hist., (5), II, p. 388 (May, 1883).

A female sea lamprey, taken by a fisherman while clinging to his boat, was opened, and its ova put into a large basin. It rained at the time and the basin became partly filled with water. After twenty days the eggs hatched into perfect larvæ. Ferry concludes: "Il resort de ce fait que les œufs pris dans le ventre de la Lamproie étaient déjà fécondés et avaient dû l'être dans l'intériéur de l'animal" (p. 722).

Gage, Simon H., and Meek, Seth E.

1886. The lampreys of Cayuga Lake (abstract). Proc. Amer. Assoc. Adv. Sci., XXXV, p. 269.

Brief reference to nests and to length of breeding season, which is said to last nearly two months (May and June).

Gage, Simon H.

1893. The lake and brook lampreys of New York, especially those of Cayuga and Seneca Lakes. The Wilder Quarter-Century Book. Ithaca. Pp. 421-493, Pls. I-VII.

Gives extended account of nest building and spawning of the brook lamprey (Lampetra wilderi) and of the lake lamprey (Petromyzon marinus unicolor); discusses fate of lampreys after spawning (pp. 441-447). Figures two lake lampreys on a nest, carrying stones—Pl. vii, Fig. 39.

Herfort, Karl.

1901. Die Reifung und Befruchtung des Eies von Petromyzon fluviatilis. Arch. f. mikrosk. Anat. u. Entwickl., Vol. 57, pp. 54-95, Pls. iv-vi.

Brief review of some European papers on spawning habits (pp. 55-57). For his own studies he fertilized the eggs artificially (pp. 57-58).

Holder, Charles Frederick.

1885. The lamprey-eel and nest. In Marvels of Animal Life; 8°; New York; pp. 5-8.

Describes how Petromyzon marinus transports stones, but mistakes the mass of stones accumulated outside the nest, for the nest itself. Quotes from an account of over fifty lampreys building near a dam in the Saco River, Maine. They dropped the stones on the dam until it became covered over. This was erroneously interpreted to mean that the lampreys had built the dam. A stone is sometimes carried by two lampreys.

Kupper, Carl v., and Benecke, B.

1878. Der Vorgang der Befruchtung am Ei der Neunaugen. Festschrift für Theodor Schwann. Königsberg.

Loman, J. C. C.

1910. De copulatie van Petromyzon planeri. Tijdschr. nederl.. dierk. Vereen, (2), XII, p. vii.

A careful account of the spawning of Petromyzon planeri, observed in a brook near Königsberg.

McClure, Charles F. W.

1893. Notes on the early stages of segmentation in Petromyzon marinus L. (americanus Le S.). Zool. Anz., XVI, pp. 367-368; 373-376.

Collected thirty specimens from a river near Princeton, New Jersey, between May 20 and June 1.

Müller, August.

1856. Ueber die Entwickelung der Neunaugen. Ein vorläufiger Bericht. Arch. f. Anatomie, Physiol. u. wissen. Medicin, Jahrg. 1856, pp. 323-339.

This is the earliest account of the breeding habits of the lamprey. The observations were made on the brook lamprey; sometimes ten or more were seen together tugging at, and transporting stones. The object for which the stones were carried was, however, not made out. He made the discovery, by rearing Ammocometes, that they are the larve of lampreys.

Reighard, Jacob.

1903. An experimental study of the spawning behavior of Lampetra wilderi. Science, N. S., XVII, p. 529 (abstract).

No constant relation between individual fish and individual nests. Location of nest is determined not by character of bottom, but by "existence beneath or in the midst of the running water of small masses of water at rest," e. g., in depressions or in vicinity of obstructions.

1908. Photography of aquatic animals in their natural environment. Bull. U. S. Bureau Fisheries, XXVII, pp. 43-68, Pls. iii-v. Photograph of four Lampetra wilderi on a nest—Pl. iii, Fig. 2.

Vejdovsky, F.

1893. O trenî mihule (Petromyzon planeri) [Die äussere Befruchtung des Neunauges]. Sitzber. d königl. böhm. Gesell. Wiss. in Prag. Math.-naturw., 1893, article XLIX, Pl. xviii.

Observed spawning process in an aquarium containing four males and one female. Figures two specimens (Pl. xviii) in copulo, but this figure does not represent them in their characteristic attitudes.

Vieira, Lopes

1831. Remarks on the eggs and spawning-season of Petromyzon fluviatilis Linn. Ann. de Sciencias Naturæs, I, pp. 79-83. Sea lamprey enters rivers of Portugal at end of December and beginning of January.

Yarrell, W.

1831. Remarks on the Eggs and Spawning-season of Petromyzon fluviatilis and P. marinus. Proc. Committee of Sci. and Corresp. Zool. Soc. London, Part I, pp. 133-134.

Examined specimens of *P. fluviatilis* weekly from March to middle of May. Up to April 19, there were more females than males; thereafter males outnumbered females, two to one. Specimens taken April 26, appeared ready to spawn. By May 10, nearly all examined had spawned. Seven specimens of *P. marinus* were taken in the Severn on May 3—"about which time they ascended that river for the purpose of spawning."

Young, Robert T., and Cole, Leon J.

1900. On the nesting habits of the brook lamprey (Lampetra wilderi). Amer. Naturalist, XXXIV, pp. 617-620.

Notes on nesting observed in two small tributaries of the Huron River near Ann Arbor, Michigan. Males precede females in beginning the nest. Nests are 7½ inches in diameter and situated anywhere in river.

Ziegler, Heinrich Ernst.

1902. Lehrbuch der vergleichenden Entwickelungsgeschichte der niederen Wirbeltiere.

Résumé (pp. 74-75), and bibliography (pp. 74, 89-91).

SHORTER ARTICLES AND DISCUSSION

A SIMPLE TEST OF THE GOODNESS OF FIT OF MENDELIAN RATIOS

In actual experimentation the so-called Mendelian ratios, 3:1, 9:3:3:1, 9:3:4, 9:7, 15:1, 27:9:9:9:3:3:3:1, etc., are never exactly realized because of the errors of sampling inherent in all statistical work. Notwithstanding this fact, the best theoretical formulæ must be selected on the basis of these misleading experimental results.

Now the test of the validity of any Mendelian formula is twofold: the number of individuals found should agree with the number expected within the limits of experimental error,¹ the assumed germinal composition of the several groups of individuals should be capable of substantiation from a study of the soma of their offspring.

For the most part, Mendelians have been satisfied to judge the goodness of fit of the theoretical frequency to the empirical by inspection merely. More recently, however, attempts have been made to apply scientific tests to this problem. The first was that of Weldon,² but Professor Johannsen doubtless deserves the credit of having interested the few Mendelian workers who have taken the pains to calculate probable errors in this indispensable part of their work.

The test used by Professor Weldon and recommended in a much extended form by Professor Johannsen³ is essentially the determination of the probable error of the number of individuals in one of the subgroups by the formula

$$S.D. = \sqrt{n \times p \times q},$$

where p is the chance of occurrence of an individual of any class, q = 1 - p, and n is the number of individuals. Thus the

¹In some cases, valid reasons for discrepancy between calculated and observed frequencies may be shown. These factors should then be taken into account in calculating the theoretical numbers.

² Weldon, W. F. R., ''Mendel's Laws of Alternative Inheritance in Peas,'' Biometrika, 1: 228-254, 1902, especially pp. 233-234.

^{*} Johannsen, W., "Elemente der Exakten Erblichkeitslehre," pp. 402-410, 1909.

"probable error" of the number of individuals of any class, say p, is

$$Ep = .67449 \sqrt{npq}$$
.

Now while Professor Weldon's use of this formula for the simple 3:1 ratios seems quite proper, the same can not be said for Professor Johannsen's generalization. This is true for three reasons:

(a) The formula is valid only when neither n, p nor q is small. In polyhybrid ratios p or q may be relatively small. It is then quite idle to use the probable error suggested, unless n be large, which unfortunately is generally not the case.

(b) Even when p is not so low as to render the use of the conventional formula for the probable error open to question, it is very laborious to calculate the probable errors for the frequency of each class.⁵

(c) It is not only cumbersome and laborious, but theoretically unjustified to test the validity of a given ratio by the determination of the probable error of one or of all of its individual component groups. The random deviations of the class frequencies are not independent, but correlated. We must have a usable criterion of the goodness of fit of the theory to the data as a whole

Such a criterion was furnished several years ago by Pearson.⁶ Its applicability to the problem of testing the goodness of fit of Mendelian ratios seems obvious, but since, as far as I can ascertain, it has nowhere been applied to this problem, it seems worth while to call the attention of students of genetics to its usefulness.

$$\chi^2 = S\{(o-c)^2/c\},$$

where o is observed frequency of any class, c is calculated frequency on the basis of Mendelian theory and S indicates a summation for the several classes distinguishable in the ratio under consideration.

P, a measure on the scale of 0 to 1 of the probability that

For example, Johannsen (loc. cit., p. 405) tables values for p=3/4, q=1/4 to p=63/64, q=1/64.

⁵ See, for instance, the example given by Johannsen, loc. cit., p. 396.

⁶ Pearson, K., "On the Criterion that a Given System of Deviations from the Probable in the Case of a Correlated System of Variables is Such that it Can be Reasonably Supposed to have Arisen from Random Sampling," Phil. Mag., 50: 157-175, 1900.

the deviations from the theoretical frequencies may be reasonably supposed to be due to the errors of sampling, may be calculated from χ^2 by formulæ which need not concern us here, since its values for systems of frequency of 3–30 classes have been tabled.⁷ Hence the Mendelian has only the simple task of calculating χ^2 and looking up the value of P in Elderton's tables.

Illustrations will make method of computation and usefulness most clear.

ILLUSTRATION I. DOUBLENESS AND PLASTID COLOR IN STOCKS Saunders, Journ. Gen., 1: 349-350, 1911

	Obs.	Calc.	o-c	(0-c)2	(o-c)2/c
Singles, White	1,666 773 790	1,615 807 807	51 -34 -17	2,601 1,156 289	1.611 1.433 .358
	3,229	3,229	0		$\chi^2 = 3.402$

Whence, from the tables in Biometrika, and by interpolation,

$$n'=3, \chi^2=3, P=.223130$$

 $n'=3, \chi^2=4, P=.135335$
Diff.=.087795
 $P=.223130-.087795 \times .402=.1878.$

Thus only in about one case in five would the errors of sampling lead to divergences from theory as bad as this. The theory is, as far as this evidence goes, *possible*, but certainly not demonstrated.

ILLUSTRATION II. SEED FORM AND COLOR IN *Pisum* Bateson and Killby, Report Evol. Com., 2: 77, 1905

	Obs.	Calc.8	0-c	(o-c)2/c
Round, Yellow	4,926	4,883	+43	.3787
Wrinkled, Yellow	1,656	1,628	+28	.4816
Round, Green	1,621	1,628	- 7	.0301
Wrinkled, Green	478	542	-64	7.5572

 $\chi^2 = 8.4476$, P = .0384. Thus taking the data as they stand, it is impossible to regard the 9:3:3:1 ratio as satisfactorily

⁷ Pearson, *loc. cit.*, gives a small table. A much more comprehensive one is given by W. Palin Elderton, "Tables for Testing the Goodness of Fit of Theory to Observation," *Biometrika*, 1: 155-163, 1901.

^{*}These are not the calculated frequencies given by Bateson and Killby, but have been recalculated as closely as possible on the 9:3:3:1 ratio. Theirs are nine seeds short.

describing the facts. But the great factor in the magnitude of χ^2 is the deficiency in the wrinkled green seeds, and the authors have suggested a reasonable biological explanation for this deficiency.

ILLUSTRATION III. COLOR IN OATS
Nillson-Ehle, fide Baur, Einf, Exp. Vererbungsl., pp. 66-67

	Obs.	Calc.	o-c	(o-c)2/c
Schwarzspelzig	418	420	-2	.0095
Grauspelzig	106	105	+1	.0095
Weissspelzig	36	35	+1	.0286

Thus $\chi^2 = .0476$ only. P is not tabled for $\chi^2 < 1$, since the probabilities of such deviations being due simply to errors of sampling are so enormously high. Theory and observation could hardly agree more perfectly.

ILLUSTRATION IV. BODY COLOR IN *Drosophila*Morgan, *Journ. Exp. Zool.*, 13: 35, 1912

529	- 4	.030
000		
265	+75	21.226
265	-71	19.023
ŀ	265	265 -71

Here χ^2 is over 40, the odds against the deviations, being due to errors of sampling, are so enormously great that it is idle to express them in figures. In short, the facts do not substantiate the hypothesis, and Professor Morgan has himself suggested possible reasons for the disagreement.

ILLUSTRATION V. PARTIAL GAMETIC COUPLING IN SWEET PEAS Bateson, Saunders and Punnett, Rep. Evol. Com., 4: 11

	Observed Number of Cases	Calculated on 7:1:1:7 Basis	Calculated on 7:1:1:7 Basis	15:111:75
Purple, long	493	471	490	
Purple, round	25	40	20	
Red, long	25	40	20	
Red, round	138	130	151	

For the 7:1:1:7 basis, $\chi^2 = 12.7699$, P = .0053. For the 15:1:1:15 hypothesis, $\chi^2 = 3.6375$, P = .3086. Thus the

chances are about 995:5 or 199:1 against the validity of the first hypothesis and only 69:31, or about 2:1, against the second.

ILLUSTRATION VI. COLOR INHERITANCE IN Antirrhinum Wheldale, Marryat and Sollas, Rep. Evol. Com., 15: 15

	Obs.	Cale.	0-c	(0-c)2/0
I. Magenta	399	361	+38	4.000
I. Magenta delila	122	120	+ 2	.033
I. crimson	121	120	+ 1	.008
I. crimson delila	38	40	- 2	.100
T. ivory	88	120	-32	9.075
T. ivory delila	35	40	- 5	.625
T. yellow	33	40	- 7	1.255
T. yellow delila	19	14	+ 5	1.786
	855	855	γ2	=16.852

Hence, P = .0185 or the chances are about 980:20 against such discrepancies being chance deviations from the theory. Thus either the theory must be discarded or reasons for the discrepancies found.

A conspicuous advantage of this method of Pearson is that in its application the deviation of observation from theory for each class and the amount which this discrepancy contributes to χ^2 are under the worker's eye.

If used with the caution that should be exercised in the drawing of any conclusion from probable errors, I believe that this well-known criterion of goodness of fit will prove most useful to Mendelians.

J. ARTHUR HARRIS

Some biologists apparently seem to feel that the calculation of a statistical "probable error" covers all the biological sins which may be committed in the collection or manipulation of their data.

NOTES AND LITERATURE

NOTES ON ICHTHYOLOGY

In the Annals of the Carnegie Museum, Vol. VII, 1911, Professor Edwin C. Starks gives the result of the survey of San Juan Island in Puget Sound. Professor Starks regards Hexanchus corinus from this region as identical with Hexanchus griseus, a view already suggested by Mr. Regan. He regards Raja stellulata as a valid species. Raja kincaidi is identical with R. stellulata. New species as follows are described and figured: Sebastodes deani, S. clavilatus, S. emphæus. Xystes axinophrys is the young of Averruncus emmelane. Xiphistes ulvæ is identical with X. chirus. One hundred and fifty-eight species of fishes are enumerated as known to occur in Puget Sound.

In the Publications of the University of California, Vol. VIII, 1911, Edwin C. Starks and William M. Mann discuss a collection of fishes from San Diego. A new genus, Orthonopias, based on O. triacis, a new species of sculpin with a scaly back allied to Astrolytes, is described. Another new genus is Rusulus, related to Clinocottus and based on a new species, R. saburræ. Maynea californica Gilbert is a new species described from Gilbert's manuscript. Valuable notes are given on other rare species.

In Science, Vol. XXXI, p. 346, Mr. Henry W. Fowler notes that Coccogenia Cockerell and Callaway (Proc. Biol. Soc. Wash., 1902, p. 1, 90) is a synonym of Coccotis Jordan (Rept. Geol. Surv. Ohio, IV, 1882, p. 852) both being based on Hypsilepis coccogenis Cope.

In the *Proc. Ac. Nat. Sci. Phila.* for 1910, Mr. Henry W. Fowler gives a list of little known fishes of New Jersey. He has also notes on Chimæroid and Ganoid fishes. He recognizes a number of Gar pikes, instead of the three usually recorded as valid. The number is certainly greater than three, but such studies as we have been able to make would not indicate that all of those noted and figured by Mr. Fowler are really distinct species. Mr. Fowler describes as new, *Cylindrosteus scabriceps* from Leavenworth, Kansas, and *C. megalops* from Bay Port, Florida.

In the same proceedings for 1910, Mr. Fowler describes 746

Dixonina nemoptera, a remarkable new fish of the family of Albulidæ from Santo Domingo.

In the same proceedings Mr. Fowler gives notes on Salmonoid fishes, describing as new, *Stomias bonapartei* from Bonaparte's collection from Sicily, *Synodus dominicensis* from Santo Domingo, and *Synodus dermatogenys* from Hawaii.

In the same proceedings Mr. Fowler lists the fishes of Delaware.

In the same proceedings Mr. Fowler describes a new flat fish from New Jersey under the name Citharichthys micros.

In the same proceedings Mr. Fowler gives notes on the Clupeoid fishes. The new genus Heringia is established for Clupea amazonica Steindachner. Ilisha narrangansetta is described from Narragansett Bay. The subgenus Anchoviella is proposed for Engraulis perfasciatus. This group includes nearly all the species of Anchovia, and it is perhaps of generic value as distinct from Anchovia and from Engraulis. Anchovia scitula is described from San Diego, Anchovia lepidentostole from Surinam, and Anchovia platyargyrea from St. Martins.

In the same proceedings for 1911, Mr. Fowler describes new species from Venezuela and Ecuador.

In the Proc. U. S. Nat. Mus. Dr. Jordan and W. F. Thompson discuss the gold-eye of the northwest, Amphiodon alosoides.

In the *Proc. Biol. Soc. of Washington Barton A. Bean and Alfred C. Weed discuss recent additions to the fish fauna of the District of Columbia.*

In the *Bull. Wisconsin Nat. Hist. Soc.*, Vol. IX, 1911, George Wagner describes a new species of cisco from Green Lake, Wisconsin, under the name of *Leucichthys birgei*.

In Science, Vol. XXXIV, No. 879, Mr. T. D. A. Cockerell describes a new minnow from Julesburg, Colorado, under the name of Notropis horatii.

In the *Proc. Biol. Soc. Wash.* Mr. T. D. A. Cockerell discusses the scales of various fishes, concluding that the soles are not degraded flounders but degenerate descendants from some flat fish from which both have been derived. This conclusion has also been reached by Professor G. H. Parker from a study of the optic nerves of the two types.

In the *Bull. Amer. Mus. Nat. Hist.*, Vol. XXX, 1911, John Treadwell Nichols has notes on Teleostean fishes. He describes as new *Moxostoma alleghaniense* from Marshall, North Carolina. *Menidia audens* Hay from Moon Lake, Mississippi, he thinks

identical with *Menidia gracilis* from Long Island. *Blennius* fabbri Nichols, lately described as new from Florida, is the young of *Chasmodes bosquianus*. In this paper the curious fish called *Stathmonotus teckla* Nichols is figured.

In Science, December 3, 1905, p. 815, the Smooth Hound, Mustelus mustelus, is recorded from New Jersey. This European species has not been previously known from our coast.

In the Ann. of Mag. Nat. Hist., Vol. VIII, 1911, Mr. C. Tate Regan publishes a detailed classification of the Siluroidea or cat fishes.

In the same annals, Vol. IX, 1912, Mr. Regan gives a classification of the *Pediculate* fishes.

In the same annals Mr. Regan describes the structure of the Symbranchoid eels.

In the same annals, Vol. XI, 1912, Mr. Regan gives a study of the *Opisthomi*.

In the same annals, Vol. VIII, 1911, Mr. Regan gives an analysis and classification of the *Gobioid* fishes.

In the same annals, Vol. VIII, 1911, Mr. Regan gives a classification of the *Cyprinoid* fishes and their allies.

In the Sitz. Acad. Wiss. Wien, 1911, Dr. Franz Steindachner describes a number of new fishes from South America.

In the *Proc. Biol. Soc. Wash.* Dr. R. W. Shufeldt gives a valuable and interesting account of the rare pelagic fish *Pterycombus brama*. The singular *Caristius* lately described from Japan by Dr. Smith, is an ally of *Pterycombus*, and belongs to the same family.

In the *Memoirs* of the Museum of Comparative Zoology at Harvard Samuel Garman gives a classification of the *Chismopnea* or *Chimæroid* fishes. He describes *Chimæra gilberti* from Hawaii, with valuable notes on all the known species.

In the Mus. Nat. Hist. of Paris Dr. Pellegrin describes numerous fishes from Ecuador, South America.

In the Ann. Carn. Mus., Vol. VII, 1911, John D. Haseman gives an elaborate catalogue of the Cichlid fishes collected by the Carnegie Expedition to South America.

In the same annals Mr. Haseman describes and figures numerous new species from South America.

In the same annals, Vol. VII, 1911, Mr. Haseman describes new species from the Rio Iguassu, an isolated tributary of the Rio Trabernath, with its peculiar fauna.

In the Sitz. Acad. Wiss. Wien, 1911, Dr. Steindachner dis-

cusses the fish fauna of Lake Tanganyika with several new species and excellent plates.

In the Bull. Soc. Zool. of France Dr. Pellégrin describes a new Barbus from South Africa, and in the Bull. Soc. Philom., Paris, he describes a new Tilapia.

In Arch. Zool. Exper. of Paris Louis Fage discusses the small codfish of the Mediterranean, showing that capelanus is distinct from luscus and from minutus.

In the *Publ. Dept. Agric.* E. W. L. Holt and L. W. Byrne describe the fishes of the genus *Scopelus* (earlier and therefore preferably known as *Myctophum*).

In the Publ. Zool. Inst. of Lund University Nils Rosen gives an account of the reptiles and fishes of the Bahamas, an excellent piece of work. New species as follows are described: Nannocampus nanus from Andros; Garmannia rubra from Andros; Gobiesox androsiensis from Andros; Anchenopterus grandicomis from Andros. Mr. Rosen regards Holocentrus siccifer Cope and Holocentrus puncticulatus Barbour as identical with H. coruscus. He also suggests the possible identity of the genus Gymneleotris and Pycnomma with Garmannia. The supposition is that in the first named genus the ventrals being described as separated have been simply split apart, the membrane being very thin.

In the *Proc. Roy Soc. of Queensland J. Douglas Ogilby describes an interesting series of new species.*

David G. Stead in the Publications of the Department of Fisheries of New South Wales gives a valuable account of the fisheries of that region.

In the Kongl. Sven. Vet. Handl., XLVII, 1911, Professor Einar Lönnberg gives an account of the reptiles and fishes of British East Africa.

In a considerable volume published by E. J. Brill, of Leyden, 1911, Dr. Max Weber, of the University of Amsterdam, and Dr. L. F. de Beaufort give a complete index to the genera or species described and mentioned by Dr. Pieter Bleeker, the most voluminous of all writers of ichthyology. In view of the exceedingly great difficulty in getting exact references to Dr. Bleeker's works, this volume of 410 pages of names and references is exceedingly useful.

In the *Proc.* of the New Zealand Institute, 1910, Mr. Edgar R. Waite gives a record of additions to the fish fauna of that country with several new genera and species.

In the Report of the Scientific Investigations of Shackleton's British Antarctic Expedition, Edgar R. Waite describes the new species obtained.

In the Records of the Canterbury Museum Edgar R. Waite gives the scientific results of the trawling expedition of the New Zealand government. Numerous interesting discoveries are recorded.

In the Publications of the Department of Trade and Commerce of Australia, 1911, are given the results of the investigations of the steamer *Endeavour* by Mr. Allan R. McCulloch. Many interesting discoveries are recorded.

In the *Proc. U. S. Nat. Mus.* for 1912 Mr. Radcliffe gives a most interesting account of new Pediculate fishes taken by the *Albatross* in the Philippines.

In the same proceedings Dr. Hugh M. Smith describes the three Chimeroid fishes taken in the Philippines.

In the same proceedings Dr. Smith describes a new family of Notidanoid sharks. The genus *Pentanchus* differs from the others in having five branchial openings only, like the ordinary shark. In a note in *Science*, July 19, 1912, p. 81, Mr. Regan claims that this shark is merely a *Scylliorhinus* which has been deprived of a dorsal fin.

In the same proceedings Dr. Smith describes numerous Squaloid sharks from the Philippines. As to these, Mr. Regan claims that Nasisqualus is identical with Acanthidium and with Deania. Squaliolus is a valid genus.

In the same proceedings Mr. Radeliffe describes 15 new species of Amia (Apogon) and related genera from the Philippines.

In the Abhandl. Senckenberg. Naturf. Ges. Frankfurt, Vol. XXXIV, 1911, Professor Max Weber gives an account of the fishes taken in the Aru and Kei Islands with a series of excellent figures.

In *Science*, May 12, 1911, Dr. Theodore Gill gives a valuable review of Professor Thompson's translation of Aristotle's "History of Animals."

In a volume entitled "The Freshwater Fishes of the British Isles" Mr. C. Tate Regan gives a most valuable popular account of the different river fishes of Great Britain and Ireland. This is written in such a way that no person of intelligence need have any difficulty in recognizing the different species found in the British streams.

In the Abhandl. Bayer. Akad. Wiss., Munich, Dr. Victor Franz publishes a most valuable paper on the bony fishes collected in Japan by Haberer and Döflein. Many new species are described, particularly from that richest of all collecting grounds, Sagami Bay, and contains many notes of value in our study of the Japanese fauna.

In the *Publ. Imp. Univ. Tokyo* Mr. Shigeho Tanaka, lecturer in the Science College, has begun a series of figures and descriptions of the fishes of Japan. This work is extremely well done and each species is illustrated by excellent plates. There is no attempt at classification, each of the five parts now issued from April 15, 1911, to March 10, 1912, containing species valuable for his purpose, without attempt at orderly arrangement.

In the Sitz. Acad. at Vienna, 1909, Dr. Victor Pietschmann describes a new species, Hemilepidotus megapterygius from Japan.

In the *Proc. U. S. Nat. Mus.* Professor J. O. Snyder describes many new species and genera from Japan and from the Riu Kiu Islands.

In the Ann. Nat. Mus. Wien. Dr. Victor Pietschmann describes the variations of a frog fish in Japan, and also describes two species of fishes from Formosa.

In the Journal of the College of Agriculture Dr. K. Kishinouye describes new herring from the Bonin Islands, and also gives an account of prehistoric fishing in Japan.

In the *Publ. Roy. Mus. Belgium* at Brussels Professor Louis Dollo has a very interesting discussion of what he calls Ethologic Paleontology.

In the American Journal of Science Dr. Charles R. Eastman describes several new sharks from Solenhofen, in the Carnegie Museum.

In the Bull. Soc. Geol. France Dr. Maurice Leriche describes cretaceous fishes from the basin of Paris.

In another publication at Lille M. Leriche describes Stampian fishes of the basin of Paris.

In the *Memoirs of the Carnegie Museum*, 1911, Dr. Eastman gives a catalogue of the fossil fishes contained in that museum, with a description and figure of many species.

In the *Mem. Mus. Roy. Belgique* Professor Ramsey Traquair gives an elaborate and valuable account of the fossil fishes of the Weald from the Bernissart.

In the Proc. Acad. Sci. of Naples Francesco Bassani gives an

elaborate account of the fossil Berycoid fishes (Myripristis melitensis) from the Miocene at Malta.

In the *Annals de Paleontologie* M. F. Prien gives a valuable study of the fossil fishes of the basin of Paris.

In the Conn. Geol. Surv., 1911, Dr. Eastman gives a description of the Triassic fishes known from Connecticut.

In the Geol. Mag. Dr. Louis Hussakof describes several Arthrodira from Ohio.

In the *Publ. Carn. Inst. Wash.* Mr. Hussakof describes the amphibian fishes known from Permian rocks from North America.

In the Publications of the Fish Commission of Pennsylvania Dr. David Marine and Dr. C. H. Lenhart describe their observations on the thyroid carcinoma or goitre of the brook trout, and the possibility of the relation of this disease to cancer. These studies are continued in the Journal of Experimental Medicine, Vol. XIII, 1911. It is concluded that there is no evidence that goitre is either infectious or contagious, its cause probably depending on lack of or a disproportion of elements necessary for proper nutrition. This is also discussed by the authors in the Johns Hopkins Medical Bulletin, Vol. XXI, 1910.

In the Science Bulletin of the University of Kansas, Professor Ida H. Hyde gives experiments on the effects of salt injections on the blood pressure of the skate.

In the Amer. Jour. Anat. William F. Allen describes the lymphatics in the tail of a large sculpin in California.

In the Trans. Canad. Inst. Professor J. P. McMurrich gives an interesting account of the life history of the Pacific salmon.

In the *Proc. Roy. Soc. Canada* Professor McMurrich has an elaborate study of the marks on the scales of fishes by which the age of salmon may be known.

In the Publications of Stanford University, 1911, Professor E. C. Starks gives a detailed account of the osteology of the mackerel-like fishes. He shows that Leiognathus is a true Scombroid, and not in any way related to the Percoid family, Gerridæ, with which Regan has placed it. In general the relations of the families on the Scombroid group are fairly determinable by their external appearance.

In the Journal of Comparative Neurology Dr. R. E. Sheldon discusses the relation of the dogfish to chemical stimuli, and also the sense of smell among sharks. He shows that the dogfish

obtains its food chiefly through the sense of smell, which is comparable to that of the higher vertebrates.

In the Internat. Revue Hydrobiol. Leipzig, 1909, Dr. Victor Franz discusses the effect of light on the movements of Indian fishes.

In the Journal of Morphology, Dr. J. F. Gudernatsch describes the thyroid glands of fishes.

In the University of California publications Mr. Asa C. Chandler describes the lymphoid structure on the brain of the gar pike.

In the Bull. Bur. Fish. Profesor G. H. Parker describes the influence of sense organs on the movements of the dogfish.

In the Zool. Jahrb. Wiss. Mr. J. C. Loman describes the natural history of the European lampreys.

In the Arkiv. för Zool. Stockholm Nils Rosen describes the blood-vascular system of the Plectognath fishes.

In the American Journal of Physiology Professor Parker describes the integumentary nerves of fishes, their reception of light and their significance in relation to the origin of eyes of vertebrates.

In the Bull. Bur. Fish. Professor Parker describes the relation of fishes to sound.

In the AMER. NATUR., 1908, he discusses the origin of the lateral eyes of vertebrates.

In the same bulletin, 1908, he discusses the structure and function of the ear of the squeteague.

In the Century Magazine, 1910, Mr. Charles H. Townsend discusses under the head of "Chameleons of the Sea," the changes of color among fishes.

In the Bur. of Fish. documents Professor Parker discusses the effect of explosive sounds on fishes. These noises are faint under water and may startle fishes for the moment, but they have no permanent effect.

In the Journ. Exper. Zool. Dr. Francis B. Sumner discusses the color changes of flat fishes with respect to their adaptation to various backgrounds.

In the Journ. Coll. Sci. Imp. Univ. Tokyo Mr. H. Ohshima gives an interesting and valuable study of the luminous organs of different species of fishes.

In the Transactions of the American Fisheries Society Mr. John P. Babcock describes his experiments in burying the eggs of salmon and trout in gravel, the result of this being that a

much larger number of eggs hatch, and the young are more vigorous than when hatched in the ordinary way.

If the eggs of salmon are buried beneath five or six inches of sand and gravel, such eggs will hatch and the young will work their way up through the sand and gravel to the surface, and by the time they emerge they have absorbed their sacs and are then exempt from the attacks of vegetable moulds.

Mr. Babcock thinks that to follow more closely the method of nature will give more value to artificial fishery hatching.

In the Report of the Fishery Board of Scotland, 1910, Dr. H. C. Williamson gives a valuable report of the reproductive organs of different species of Scottish fishes.

In the Bull. Zool. Soc. New York Dr. F. B. Sumner continues his study on the changes of color of fishes on different bottoms. The purpose of these changes seems to be simply concealment from their enemies as well as from those fishes on which they prev.

In Knowledge, Vol. XXXIII, 1910, Rev. T. R. R. Stebbing discusses genders in zoology, sharply criticizing the carelessness with which scientific men have made what he calls "Homeric blunders," Homer being accustomed to nod when questions of classical refinement were brought before him. Mr. Stebbing proposes that in zoology every generic name, whatever its termination, should be recorded as masculine.

In the *Philippine Journal of Science* Alvin Seale gives a valuable account of the fishery resources of the Philippine Islands.

In the Biological Bulletin Victor E. Shelford gives an interesting account of experiments on stream fishes and pond fishes.

In the Bureaus of Fisheries Document 733 William C. Kendall discusses the American fishes, their habits and value.

In Science, October 11, 1911, Professor E. C. Starks discusses the structure of the air bladder in Ophicephalus.

In *Science*, Vol. XXXIII, 1911, Mr. Starks discusses the origin of the gobies. He regards them as somewhat allied to the sculpins.

In the First Annual Report of the Laguna Marine Laboratory of Pomona College, Claremont, California, are numerous excellent papers on the local fauna of Laguna Beach in southern California. Among these papers is an elaborate and well-planned study of the fishes of the tide pools, by Charles W. Metz. The report is accompanied by excellent plates.

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